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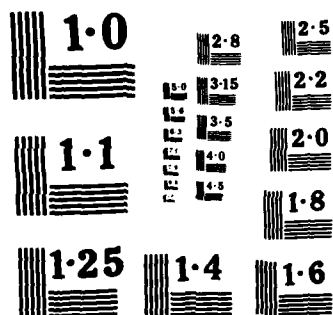
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OLD DOMINION UNIVERSITY
NORFOLK, VIRGINIA 23508

BIOLOGICAL ACTIVITY AT OCEANIC FRONTS

By

William M. Dunstan, Co-Principal Investigator

and

Kimberley Davis, Co-Principal Investigator

Final Report
For the period ended September 30, 1984

Prepared for the
Biological/Chemical Oceanography Branch
Oceanography Division (Code 333)
Naval Ocean Research and Development Activity
NSTL, Mississippi 39529

Under
Research Contract N00014-84-K-0283
Dr. Denis Wiesenburg, Scientific Officer

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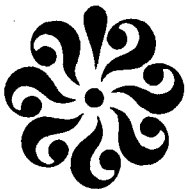
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Introduction

Oceanic fronts, the sharp transition regions between different water masses, exhibit enhanced biological activity, ^{which can be} that is of interest to scientists and laymen alike. The observation that fronts are dynamic sites of intensified motion and biological productivity is not new. The 19th century American oceanographer Matthew Maury described a front as a "wonderful phenomenon on the sea." The description of a front as being "the collision and the struggle of two currents" was made by G. F. Neumeyer in 1875. Even Biblical references to the existence of fronts have been noted (Bowman, 1978).

On Beebe's 1926 Arcturus Expedition (approximately 400 miles southwest of Panama), he observed that, "A few scoops with a hand net would collect a mass equal to a long haul through average ocean water, ...yet ten yards on either side of the central line of foam, the water was almost barren of life." He also saw aggregations of plankton, fish, birds, and dolphins.

For centuries, fishermen have been aware that fronts are productive fishing grounds and may be located by the characteristic foam lines and flotsam at the sea surface and birds foraging close by. Sailors have likewise known that frontal boundaries may produce choppy, erratic seas in even mild weather and dangerous, challenging seas in storms. Japanese sailors have referred to a front as a "siome" and the mature sea state it evokes in high winds, denoted by confused and steep pyramidal waves, as "sionami."

Observations of the hydrodynamics and biological nature of fronts were carefully documented by the Japanese oceanographer Michitaka Uda (1938, 1959). He noted the accumulation of foam, detritus, flotsam, and

members of the marine food chain from phytoplankton to zooplankton, fish, birds, and marine mammals and contended that phytoplankton growth at fronts is enhanced, particularly in the spring. A second major biological consequence of fronts was described: "fronts act as faunal and floral boundaries limiting the distribution of organisms in much the same way as zoogeographical features of the shores and sea bottoms."

Uda's observations pioneered the modern study of fronts. Unfortunately, the limitations of early oceanographic sampling methods tended to obscure rather than elucidate oceanic variability. Intermittant hydrocasts often missed such oceanic features as fronts, making the ocean appear relatively homogeneous horizontally. The advent of high resolution and synoptic sampling (such as continuous sampling and remote sensing) has exposed sharpened oceanic features and strong property gradients. High variability has been shown to extend not only vertically, but in the horizontal dimension as well. With the increased interest in (and funding for) measuring optical parameters, biological oceanographers have obtained new tools for studying phytoplankton, the principal attenuators of light in the open ocean, and physical oceanographers have found new methods for tracking oceanic circulation. With these new approaches, two aspects of frontal study have become clear: 1) fronts are ubiquitous features in the ocean and 2) the biology and the hydrodynamics of the frontal system are tightly coupled. To assess the biological activity of a complex frontal system, researchers necessarily employ interdisciplinary strategies.

Through these research efforts, it has become evident that fronts are areas of high biological activity that can:

- 1) mechanically concentrate and/or sort various plankton and particulate substances, including pollutants;
- 2) stimulate increased autotrophic and heterotrophic productivity, including red tide conditions;
- 3) affect behavioral patterns such as diurnal vertical movements of plankton and migration of oceanic fishes,
- 4) juxtapose communities that otherwise would not interact, forming new community assemblages, and
- 5) limit the distributions of various organisms, serving as biogeographical boundaries.

Thus, biological activity at fronts has important ramifications to the marine ecosystem. The effects of frontal biology extend to other aspects of oceanography as well since various chemical, acoustic, and optical parameters are biologically mediated. Also, information concerning paleo-circulation and paleo-climatic conditions can be gleaned from the deposited remains of frontally concentrated organisms. These biological patterns are useful in constructing predictive models of ocean hydrodynamics. Therefore, the study of biological activity at fronts yields information valuable to a variety of members of the oceanographic community.

Types of Fronts

Fronts occur anywhere in the ocean that boundary conditions exist: at the sea surface or below, nearshore or offshore. Appearing on all spatial scales, fronts range from less than a meter, having only localized environmental impact, to planetary scale, influencing weather and climate. Some fronts, such as western current boundaries, are

relatively permanent features while others, such as estuarine fronts, are episodic or highly ephemeral.

There are various factors that incite boundary conditions: density, velocity, or turbidity gradients, topography, and atmospheric forcing. Any one or combination of these can result in an oceanic front. Bowman (1978) categorized major frontal systems on the basis of their principal driving forces. A modified version of this frontal scheme is presented in Table 1 along with typical spatial and temporal scales.

A factor that most frontal systems have in common is the existence of property gradients such as temperature, salinity, or turbidity. Of importance in many frontal systems, differential heating and cooling and the influx of fresh water at oceanic boundaries cause horizontal discontinuities of salinity and temperature. The interface of these juxtapose water masses of different salinity and temperature is termed the front. The actual locations of such property fronts, that is the salinity front and the temperature front, are not necessarily coincident. Indeed, the true location of a single property front is that of the maximum attained gradient (Roden, 1976). Furthermore, these fronts are not necessarily baroclinic (exhibiting a density gradient) depending on whether the density field is reinforcing or compensating. This condition is seasonally variable in some cases.

Locally, meteorological processes modify these signatures (via heating, cooling, evaporation, and precipitation) creating interspersed lenses of different densities. The recent advent of satellite imagery has illustrated the typical non-uniformity in strength of the thermohaline gradients. The intermittent segments of strong and weak

gradients result in meanders and eddies along the frontal boundary (Roden, 1976).

Differences in the current velocity fields (speed and/or direction) of adjacent waters are frequent frontal determinants, particularly when inertial and frictional forces are in effect. The resultant hydrodynamics of a velocity front and frequently a property front is convergence and consequent downwelling at the interface or less frequently, divergence and consequent upwelling. Convergence is often visibly evidenced by foam and detritus lines along the surface while divergence results in sea slicks. Frontal systems therefore exhibit higher vertical advection than open ocean areas.

Satellite imagery is helpful in determining the genesis of different fronts. Of the various detectors, infrared radiation identifies temperature fronts, specular optics detects differences in sea state, identifying velocity fronts, and color contrasts indicate differences in the quality and quantity of suspended particulates (Maul and Gordon, 1975).

The frontal types as distinguished by Bowden in Table 1 are derived from one or a combination of these origins. Open ocean, planetary fronts result from atmospheric forcing and are located distant from other major boundaries. Caused by the convergence of Ekman transport systems, they are best developed in the surface layer. They are strongly associated with regions of high positive wind shear. Roden (1975) cited the subarctic front of 42 degree Latitude of the central Pacific as an example. At this boundary, colder, lower salinity subarctic water is separated from warmer, higher salinity central

Pacific water to the south. Baroclinicity is low due to compensating salinity and temperature gradients.

The structure of heat and salt flux fields often results in convergent fronts that in spring and fall may be coincident with Ekman transport convergences. These relatively shallow phenomena are associated with edges of cloud cover, precipitation, and wind. The temperature and salinity fronts usually do not coexist, therefore baroclinicity is high. A mid-Pacific doldrum front was described by Roden (1974) as separating a rainy doldrum area from adjacent, drier trade wind areas. Here, a salinity front exists in the absence of a thermal front. This is one of the few oceanic regions where only salinity determines the density field.

Western boundary current fronts occur when warmer, saltier water of tropical origin intrudes into higher latitudes. These regions, such as the Gulf Stream wall and that of the Kuroshio, are highly baroclinic and exhibit deep frontal structure.

Estuarine, plume, tidal, shelf-break, and upwelling fronts are nearshore features of varying spatial and temporal scales and are, except for plume fronts, typically affected by bottom topography.

Shelf-break fronts occur at the interface of shelf and slope waters. They are best developed in surface structure where a steep shelf to slope transition exists, generally between 100 and 300 m in depth. The extent of the baroclinicity of such fronts depends on the coincidence of the temperature and salinity fronts and whether the contributions of each compensate or reinforce the density field. These fronts were described in detail by Dickson et al. (1980) and Pilbeee and

Mande]] (1981) and were divided into two categories, prograde and retrograde, by Mooers et al. (1978).

Prograde fronts separate higher salinity shelf water from lower salinity offshore water. Such conditions exist during upwelling events on the shelf. Offshore or alongshore winds force surface waters away from shore, allowing colder, higher salinity water to surface from below. An upwelling front may be envisioned as the surface manifestation of an inclined pycnocline (Figure 1). Periodic breaching or relaxation of upwelling fronts occurs seasonally or episodically and releases nutrients and biota to offshore waters. Such fronts are exhibited off the U.S. west coast, Peru, and northwest and southwest Africa.

Retrograde fronts separate lower salinity shelf water from higher salinity offshore water. The shelf water is diluted with terrestrial runoff the extent of which is seasonally variable. Like prograde fronts, retrograde fronts separate colder nearshore from warmer offshore water.

Simulating this retrograde structure, estuarine fronts (Figure 2) result from advection of lower salinity water in channels past higher salinity shoal water. The consequent salinity gradient may be quite pronounced. In Delaware Bay, one meter's distance displayed a 4 ppt change in salinity (Klemas and Polis, 1977). These features extend parallel to the long axis of the estuary for distances of tens of kilometers and are highly ephemeral, persisting on the order of only hours. Figure 3 illustrates estuarine frontal structure. Shoaling areas are the sites of these fronts, where tidal stirring due to bottom topography is strong enough to disrupt any vertical stratification

(Bowman and Iverson, 1978). An important factor in the maintenance of this type of front is lateral shear at the interface, a phenomenon that varies in intensity with the tidal cycle. Ebb tide produces stronger shear with higher gradients and surface convergence, while at flood tide the front dissipates.

Plume fronts, such as the Columbia, Amazon, and Hudson, are also retrograde in structure. They occur at riverine plume edges that have intruded into coastal waters and typically exhibit strong turbidity gradients. In cases of high discharge rates, the plume edge extends some distance into the coastal ocean, spreading as a buoyant mass overtop of the receiving water as shown in Figure 4 (Bowman and Iverson, 1978). Friction at the plume/coastal water interface causes a sharp front to form. In cases of low discharge rates and strong, reversing tidal flows, fronts appear only at ebb tide, dissipating at flood tide.

Tidal (shallow sea) fronts occur in estuaries and nearshore waters, around shoals, islands, peninsulas, and capes. They delineate the boundary of shallow, tidal and wind mixed waters and deeper, offshore waters that are vertically stratified. Manifested at the surface by convergence zones, they respond to the neap and spring tidal cycle. Their positions are predictable from just two parameters, depth and tidal stream velocity (Simpson and Hunter, 1974; Pingree and Griffiths, 1977). Examples include the Celtic and Irish Seas and approaches to the English Channel (Simpson and Pingree, 1978; Pingree et al., 1974), Long Island and Block Island Sounds (Bowman and Esaias, 1981), and Hecate Strait (Perry et al., 1983) and the Strait of Georgia (Parsons et al., 1981), British Columbia.

Particle Accumulation

Hydrodynamic processes that cause particle and plankton accumulation and differential sorting can be examined on a very localized level. Thermally and wind-induced areas of vertical motion forming convection cells are two mechanisms that cause patterns in entrained particles.

Uneven heating and cooling at the sea surface creates alternating areas of convergence with downwelling and divergence with upwelling separated by cells of relatively little motion called Benard cells (Figure 5). Streaks of accumulated particles and small organisms are generally located 6 to 8 times the depth of the bottom (or thermocline) apart. Strommel (1949) predicted the results of entrainment of various passive particles into these Benard cells (Figure 6). Areas of upwelling collect the non-motile, positive sinking velocity organisms while areas of downwelling attract the motile, possibly positively phototactic or buoyant organisms. Cells are thus "sorted" into different regions according to size, buoyancy, or motility criteria. Evidenced at the surface would be those highly buoyant organisms such as Trichodesmium, those with floating mechanisms such as Sargassum, and motile plankton such as dinoflagellates (Wyatt, 1975).

Increased turbulence tends to disrupt this accumulation effect. The motion caused solely by the static instability of the water column is defined by the Defant/Hesselberg criterion, E , calculated from density, depth, salinity, and temperature values. Negative E values indicate static instability which can be maintained by evaporation at the surface leading to the formation of Benard cells (Defant, 1961).

Wind-induced motion results in convection cells similar in conformation to Benard cells called Langmuir cells. This circulation type forms with wind velocities greater than 3 m/sec (Fallen and Woodcock, 1964). Divergent and convergent flows form at an angle to the wind producing helical cells on the magnitude of Benard cells (Figure 7). The resultant effects on plankton and particles are similar to those of Benard cells and the circulation patterns derived from these two different driving forces are typically not distinct in the ocean (Wyatt, 1975).

A modification of the Defant/Hesselberg criterion yields Ri , the Richardson number, indicative of the stability of a turbulent medium. High Ri values indicate low turbulence, conditions conducive to accumulation of positively phototactic plankton at the surface though not in linear streaks. With increased wind stress and somewhat lower Ri values, there is a tendency towards formation of linear streaks characteristic of Langmuir cells.

Wyatt (1975) suggested that the plankton assemblage present is constrained by the typical range of Ri values encountered. For example, in a high Richardson number environment, non-motile cells of high sinking velocity fall out of the water column. Small scales fronts in convection cell structure may be important in maintaining cells in the water column and ultimately determining those that can survive there.

Dufour and Stretta (1973) suggested that particle accumulation due to convergence is one explanation for the high phytoplankton biomass observed at thermal fronts. Various studies support this view, although many only speculate on the mechanisms that cause the observed particle accumulations. Whether hydrodynamic forcing or in-situ production is a

more important mechanism, increased particle concentrations relative to lower background values are a typical characteristic of fronts of various spatial and temporal scales.

Strong surface convergence of velocities on the order of 10-20 cm/sec were observed to entrain particles including detritus and buoyant organic matter (Klemas and Polis, 1977). Distinct changes in water color and clarity often accompanied by lines of foam and flotsam (Figure 8) serve as visible clues in locating convergent fronts (Klemas and Polis, 1977; Bowman and Iverson, 1978). These different color signatures of frontally separated waters are visible from remote platforms (aircraft or satellite) and reflect differences in suspended sediment and/or phytoplankton concentrations between the adjacent areas.

High particle concentrations are associated with a front east of the Galapagos Islands, a feature possibly caused by the confluence of the Peru current with the south equatorial current (Pak and Zaneveld, 1974). Earlier investigations revealed the same front, indicating its permanence. Owen (1981) suggested that it is the same feature described by Beebe (1926) as being a site of intense biological activity.

Fournier (1978) described increased phytoplankton biomass at the Nova Scotian shelf-break front, the physical gradients of which are quite pronounced at times, up to 6 degrees C and 2 ppt over 3-5 km. Maximum chlorophyll *a* values at the front were 4.2 mg/m³ compared to background values of less than 1 mg/m³.

Direct visual observations of the effects of convergent flow on entrained plankton were made by Pingree et al. (1974) in a tidal (shallow sea) front in the English Channel. Most interestingly, a small jellyfish caught in the downwelling zone sank 20 m in about 20 sec. Net

tows revealed accumulations of various crustacean groups and other zooplankton in the frontal region that exceeded resident concentrations on either side.

Concentrations of Trichodesmium 80 km long were recorded at an estuarine front off Japan (Iisuka and Arie, 1969) and similarly accumulations of Noctiluca scintillans occurred off Brittany (Lefevre and Grall, 1970).

Convergent flow at a plume front was described by Bowman and Iverson (1978). Accumulated debris at the Hudson River plume front coincided with the 29 ppt isohaline. Convergent currents entrained oil, tar balls, bottles, derelict boats, timber, and garbage. They also found chlorophyll fronts coincident with the salinity fronts at the plume's edges.

The same hydrodynamic processes that cause enhanced plankton and particle concentrations at convergent fronts are involved in trace metal/pollutant enrichment in these areas. A marked salinity front off the Scottish coast was accompanied by increases in inorganic nutrients and dissolved trace elements including Cd, Cu, Mn, and ²²⁶Ra above background values (Kremling, 1983). Szekielda et al. (1972) found concentrations of Cr, Cu, Fe, Hg, Pb, and Zn to be 4 orders of magnitude higher in foam collected from Delaware Bay frontal convergence zones than in average ocean water. These results compare favorably with predicted values for metal enrichment in sea surface microlayer studies, taking into account that additional enrichment at downwelling zones occurs should occur. In a study of the same area, Sick et al. (1978) determined the concentrations of selected dissolved metals to be higher in samples from the front than in surrounding water. They suggested

that the mechanism for this accumulation of dissolved species is advective entrainment of dissolved metals adsorbed to particulates of less than 0.45 μm . That these metals are incorporated into the food chain was determined by examining the concentrations in the zooplankton.

Enhancement of Plankton Biomass and Production

Both small scale convection cell fronts and larger scale convergent fronts cause particle and plankton accumulation. However, studies have shown that phytoplankton, once entrained into the frontal zone, flourish and that this enhanced production is transferred up the marine food chain.

The front types that have been more intensively studied are shelf-break and shallow sea (tidal) fronts. A question central to productivity investigations is whether actual frontally-enhanced growth is in effect because in any case of increased standing crop, phytoplankton need only grow as fast as surrounding non-frontal assemblages to exhibit increased productivity. In one of several studies of the Nova Scotian shelf-break front, Fournier et al. (1977) discerned a trend of increased phytoplankton growth rates (determined as 250 times ATP in doublings/day) at the station closest to the front in cross-shelf transects. This indicates that high production per unit biomass occurs, irregardless of the degree of accumulated biomass. Shelf-break growth rates were, in several instances, higher than the maximum expected, indicating that ideal growth conditions exist at the shelf/slope transition zone for an extended time or for many shorter intervals. It was suggested that the input of nutrients via vertical turbulence stimulates enhanced phytoplankton activity. A consistent

relationship between relative chlorophyll fluorescence (in vivo) and temperature across the front was also observed. This trend was evident in both periods of strong vertical stability (May and August) and in times of intense vertical mixing (March). It was contended that a frontally localized net vertical flux of nutrients causes high frontal phytoplankton biomass when adjacent areas are nutrient limited. The source of this input may be intermittent subsurface intrusions of nutrient-rich slope water.

Herman and Denman (1979) studied tidal intrusions onto the Scotian shelf as a source of nutrients. Nitrate concentrations in the slope water below the shelf-break front were high (greater than 4 mg at/m³) while levels above the interface were relatively low (0.4 mg at/m³) due to depletion by the spring bloom. Concentrations within the front and chlorophyll maximum were intermediate, implying that nutrient depletion in the surface is offset by nutrient replenishment from below.

A follow-up investigation to Fournier et al. (1977) was undertaken by Fournier (1978) to account for the increased March chlorophyll levels exhibited at the front, a condition in which nutrients in surrounding waters are not limiting. The results indicated that a reduction in the depth of the mixed layer occurs at the front due to the mixing of the two water masses. This causes an apparent increase in the light levels available to phytoplankton in this frontal region of shallow stratification.

Fournier et al. (1979) later showed a correlation between the inclination of the subsurface frontal structure and the concentration of chlorophyll a. In winter, high nutrient, light-limited conditions are resolved with increased inclination of the front. It was calculated

that, under ideal winter conditions (strong frontal inclination), an increase in annual production at the front could result from as little as 35 days of intermittent growth.

In the summer, the shelf-break front of the New York Bight is non-baroclinic (thermohaline gradients are density-compensating). An abrupt change in the depth of the chlorophyll maximum coincides with the front (Houghton and Marra, 1983). In the absence of frontal density structure, this phenomenon is attributable to cabbeling and double diffusion which enhance vertical mixing.

A summary of the seasonally variable shelf-break frontal effects on phytoplankton activity is as follows. In late winter and early spring when nutrients are plentiful near the surface, increased inclination of the subsurface frontal structure optimizes the light regime for phytoplankton (Fournier, 1978). Later, with nutrients depleted at the surface and the frontal structure still baroclinic, tidally-forced intrusions of slope water onto the shelf introduce nutrients (Herman and Denman, 1979). Finally in summer, when the front has lost its density gradients, processes of diffusion and cabbeling become important to phytoplankton success (Houghton and Marra, 1983).

Increased productivity due to divergence of one or both sides of a front resulting in nutrient upwelling is a second explanation for the high frontal biomass (Dufour and Stretta, 1973). That episodic frontal eddies and intrusions of nutrient-rich water onto the continental shelf are a source of nutrients for phytoplankton was shown by Dunstan and Atkinson (1976), Atkinson et al. (1978), and Yoder et al. (1983, 1981). Atkinson et al. (1978) found blooms of Phaeocystis pouchetii in a cold intrusion of Gulf Stream water to dominate the phytoplankton assemblage.

A nearshore surface chlorophyll maximum associated with nutrients of freshwater input and an offshore maximum associated with the intrusion were evident. The nitrate maximum was at the leading edge of the intrusion indicating a delay before uptake by phytoplankton was occurring. These bottom intrusions from the Gulf Stream are characterized by relatively low temperatures, high chlorophyll *a*, and high particle concentrations (Paffenhofer et al., 1988).

Yoder et al. (1981) studied an upwelled eddy front on the southeastern shelf in which surface chlorophyll exceeded 5 ug/l, a value 10-100 times higher than the concentration in the parent Gulf Stream or the resident shelf water. Diatoms dominated this April sample. The strong chlorophyll gradients were evident via Ocean Color Scanner remote imagery (McClain et al., 1984) and contrasted sharply with the oligotrophic Gulf Stream waters.

Yoder et al. (1983) estimated that, at the outer southeastern continental shelf, seasonal primary production in intruded waters is approximately 175 gC/m²/6 mon (November to April), 50% being "new" production to the shelf. Intrusions penetrate farther onto the shelf when waters are stratified, with production values of about 5 times that of the overlying, nutrient-depleted layer. Production continues for approximately one week or until nutrient supplies are exhausted. Since upwelling events occur about 50% of the time from November to April, they are probably the single most important process governing phytoplankton dynamics on the outer shelf.

A specialized type of tidal front, the headland front, was described by Pingree et al. (1978) as forming due to deterred flow about such features as headlands, shoals, islands, and banks. Chlorophyll data

reported by Bowman and Esaias (1977) showed entrainment of phytoplankton into a jet stream originating in this manner. These fronts develop periodically, usually generating and dissipating within a tidal period. It is the short temporal and spatial scales that distinguish these fronts from shallow sea fronts. The possibility that headland fronts contribute notably to the primary production of the local ecosystem is suggested by intensive sport and commercial fishing at these sites. Entrained buoyant detritus, neuston, and zooplankton may serve as a food source for the nekton. The ephemeral nature of these fronts may reduce their importance as an original source of food, but they effectively reduce the foraging effort by concentrating food from other areas.

The biological characteristics of shelf-break and shallow sea fronts are similar although different mechanisms introduce nutrients from the deep water. Enhanced phytoplankton biomass at the numerous shallow sea fronts of the northwest European shelf is well documented (Pingree, 1975; Pingree et al., 1976; Simpson and Pingree, 1978; Pingree et al., 1978) as is enhanced primary productivity (Pingree et al., 1975; Savidge, 1976). One reason as explained by Simpson and Pingree (1977) calls for tidal stirring as the mechanism responsible for delivery of nutrients to the surface layers. Fronts serve as transition zones between well-mixed, nutrient rich waters and vertically stratified, nutrient depleted waters. At the shallow sea front, alternating periods of tidal or wind-induced mixing that input nutrients followed by stratification events allowing sufficient insolation result in enhanced phytoplankton growth. Tett (1981) developed a vertical mixing model to predict the distribution of phytoplankton across these shallow sea fronts.

Nutrient analyses at one shallow sea front revealed high levels of nitrates below the interface, approximately 2-7 mg at/m³. Above the interface, nitrate levels drop to less than 1 mg at/m³ due to depletion by the spring bloom. But at the frontal regime, the combination of sufficient light and nutrient levels optimizes conditions for phytoplankton success, sustaining the population through the summer (Simpson and Pingree, 1977). Phytoplankton accumulation at the thermocline indicates low dispersal by turbulence and quick access to upwardly fluxing nutrients. During spring tides, injection of nutrients occurs at the base of the thermocline instead of along the surface of the front due to turbulent bursting (Simpson and Pingree, 1978), a phenomenon exploited by dinoflagellates.

Pingree et al. (1979) indicated that cyclonic frontal eddies may be important to phytoplankton production in assisting transfer of nutrients across the front. A dominant organism found in a cold core eddy by Pingree et al. (1975) was Gyrodinium aureolum, in concentrations as high as 104/ml. This indicates a feasible seeding mechanism for this dinoflagellate in summer.

The nutritive processes in effect at a particular system can be inferred by determining the dominant phytoplankton groups (Pingree et al., 1978). Small chain-forming diatoms exploit mixed waters with upwelled nutrients accompanied by relatively reduced microheterotroph activity (Holligan et al., 1984). In stratified waters, low nutrient levels are partially compensated by highly active microheterotrophs that rapidly regenerate available nutrients. Flagellates of growth rates greater than 1/day succeed in such conditions. Small diatoms and dinoflagellates such as Gyrodinium aureolum frequently dominate the

frontal regime, possibly due to quick assimilation of nitrate from the thermocline base, upward movements of cells, and low grazing pressure.

High phytoplankton activity at shallow sea fronts is often accompanied by increased zooplankton concentrations over surrounding waters. Pingree et al. (1974) observed higher frontal concentrations of copepods and euphausiids in surface plankton tows at a 15 km long European shelf tidal front.

A third reason for increased frontal phytoplankton biomass was offered by Dufour and Stretta (1973). The admixing of two water types of complementary constituents may invoke positive phytoplankton response. Emphasizing the importance of nutrient limitation at fronts, Savidge (1976) revealed nitrate-limited phytoplankton growth at fronts through enrichment experiments. This indicates that overall net production may be determined by the flux of nitrate in cross-frontal and vertical mixing (Holligan, 1981). Adding support to the nitrate limitation found by Savidge (1976), Parsons et al. (1983) concluded that a rapid uptake of nitrate at the tidal front region occurs, stemming from the mixing due to spring tides. As water moves back and forth in response to the neap/spring tidal cycle, a region is defined where dispersal of phytoplankton occurs at spring tide, but stratification and conditions conducive to growth follow at neap tide. Phytoplankton exploit these brief periods of stabilization, responding with increased division rates of cells at the front (Pingree, 1978).

In a study of Saanich Inlet, British Columbia, Parsons et al. (1983) observed changes in phytoplankton biomass and productivity at the front in response to the 14-day spring/neap tidal cycle. The highest values of each parameter corresponded with neap tide, the times of reduced

water exchange. Legendre (1981) and Legendre et al. (in prep.) conclude that neither water column stabilization nor destabilization favors enhanced phytoplankton production. It is the alternation of stabilization and destabilization events that is most conducive to growth. This provides a pathway by which hydrodynamic energy increases primary production through the proximal agents of light and nutrient fluctuations.

Behavioral Responses of Nekton

Autotrophs, responding to frontal conditions that stimulate growth, constitute the foundation for an enriched food chain. That frontally-enhanced production reaches the highest trophic levels is evidenced by the attraction of top-level carnivores, including tunas, birds, and humans, to fronts in search of food. Higher animals that associate with fronts for feeding include skipjack, yellowfin, albacore, and bluefin tunas, mackerel, salmon, and some whales (Uda, 1938, 1952, 1973; Uda and Ishino, 1958).

Behavioral responses of nekton to deep sea fronts are commonly noted. Knauss (1957) saw aggregations of squid, sauries, flying fish, and lantern fish at a front crossing 120 degrees West in the equatorial Pacific. In the northern Pacific, fronts mark the northern and southern extensions of the transition zone between subarctic and central Pacific waters. The annual pattern of albacore tuna migration seems to be associated with these fronts (Shomura and Otsu, 1956; Graham, 1957). A study by Laurs and Lynn (1977) showed albacore tuna catch data in this region to be strongly correlated with the transition zone fronts (Figure 9). A highly productive saury fishery occurs in the northwest Pacific

in a series of eddies along the Kurile front (Uda, 1938; Han and Gong, 1970). This front delineates the southern extension of subarctic water, the equivalent of the polar front.

It is unclear whether foraging tuna respond to biological or physical cues in their movements. Certainly, prey abundance will retain the interest of the carnivores until supplies are depleted. However, salinity or temperature gradients may be proximal agents in determining fish movements, as Neil et al. (1976) suggested a mechanism by which tuna may sense temperature gradients as slight as 0.1 degrees C/km.

Convergent flows along the salinity front separating the North Pacific central and equatorial waters are associated with aggregations of skipjack tuna and their prey. The periodic movement of this front past the Hawaiian Islands is coincident with increased skipjack catches, indicating a biogeographic boundary exists for the fish (Seckel, 1972).

Behavioral responses of nekton have also been noted at nearshore fronts. Laurs et al. (1977) found temperature fronts caused by upwelling to affect albacore behavior. By tagging and tracking methods, it was determined that albacores associate with the front during upwelling events and cease when upwelling stops. They were observed to swim more slowly through the front and spend less time on the colder side (less than 15 degrees C), indicating that the front may be a thermal barrier.

The Columbia River plume front was studied in relation to albacore catch data. Owen (1968) found that, while albacore passed through the distinct plume boundary defined as the 32.2 ppt isohaline, catches at the plume/sea interface were higher than at mid-plume. Owen interpreted that either the albacore were attracted to the plume front or avoided

the lower salinity core while seeking out warmer water. Likewise, Percy (1973) found high catches of albacore associated with the Columbia River plume front, which indicates that the fish follow the front in their annual migration pattern.

Pingree et al. (1974) noted aggregations of higher animals at a convergent tidal front in the English Channel which included birds such as puffins, terns, and shearwaters. Marine mammals (Gaskin, 1976) also utilize tidal fronts. Minke whales were observed to feed on herring or capelin collected in fronts and fin whales fed on concentrations of euphausiids forced to surface by mackerel schools.

Ecological Importance of Fronts

While the study of biological activity at fronts is important to many different members of the oceanographic community, the ramifications of frontal biology to the marine environment are perhaps more crucial.

Of local and sometimes widespread importance, red tides may develop due to the seeding effect of fronts on dinoflagellate blooms. Current and future studies will evaluate this tightly coupled bio-physical relationship more thoroughly and assess its significance to the marine ecosystem.

It has been shown that frontal convergent flows accumulate particles and plankton, including trace metals and pollutants. It is also evident that frontal conditions incite enhanced productivity that is reflected up the food chain. It is important that future studies assess the significance of frontal contributions to global production, with particular respect to the potential impact of frontal-paternal pollutants on fisheries and human health.

Table 1
Classification of fronts (Bowman, 1978)

Type of Front	Major Driving Force	Scale
Fronts of planetary scale	Convergence of surface Ekman transports	1000's of kms
Fronts representing the edge of major western boundary currents	Intrusion of warm, salty water of tropical origin into higher latitudes	1000's of kms
Shelf break fronts	Density differences between shelf and slope waters	100's of kms
Upwelling fronts	Offshore surface Ekman transport associated with alongshore wind stress	10-100's of kms
Plume fronts	Density difference between river and coastal water	10-100's of kms
Shallow sea fronts	Density difference between shallow, mixed nearshore water and stratified deeper offshore water	10-100's of kms
Estuarine fronts	Lower salinity water in the channels is advected past higher salinity shoal water	10's of kms

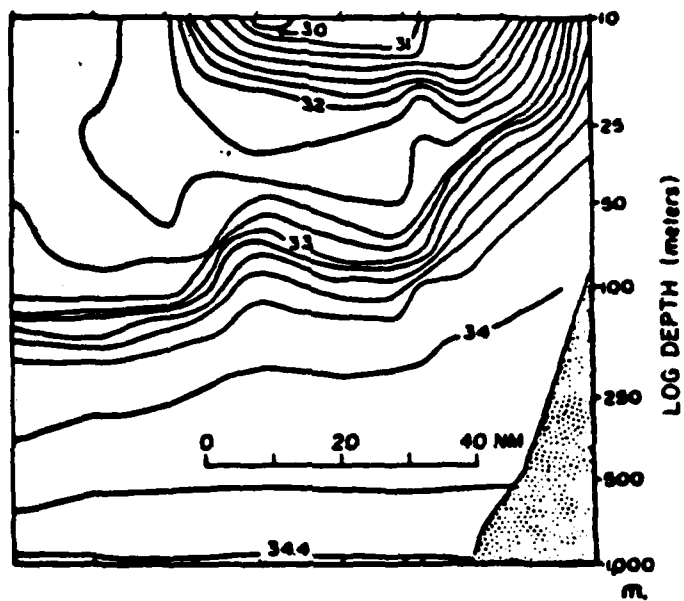


FIGURE 1. Structure of a prograde (upwelling) front. Owen (1968)

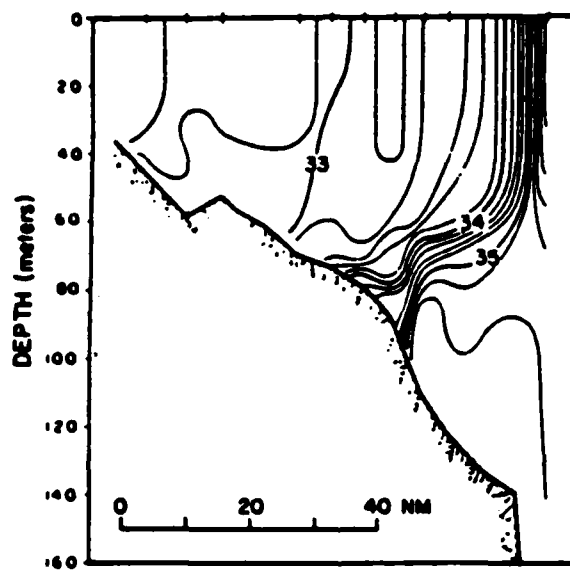


FIGURE 2. Structure of a retrograde (estuarine) front. Mooers et al. (1978)

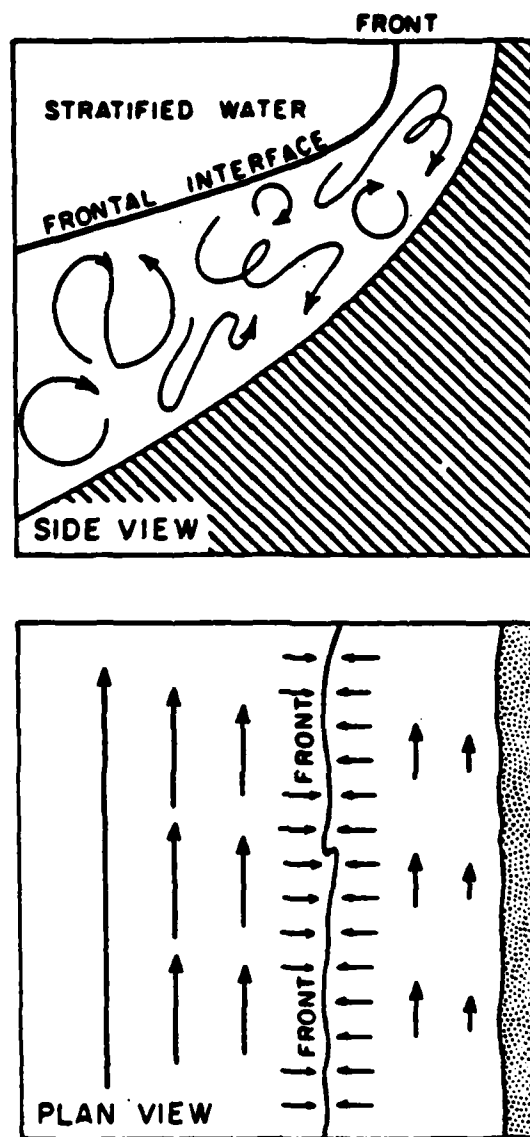


FIGURE 3. Schematic diagrams of an estuarine front. Streamlines represent bottom stirring. Bowman and Iverson (1977)

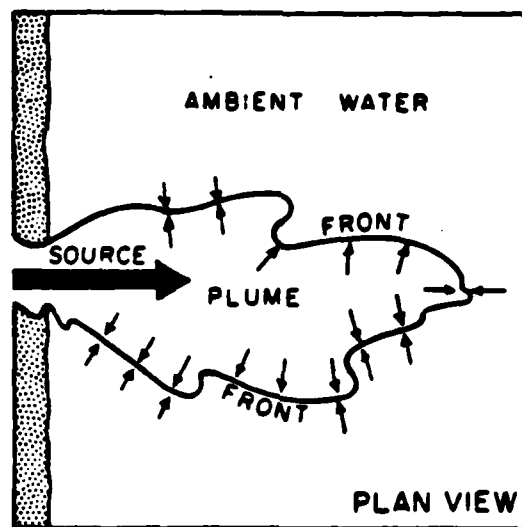
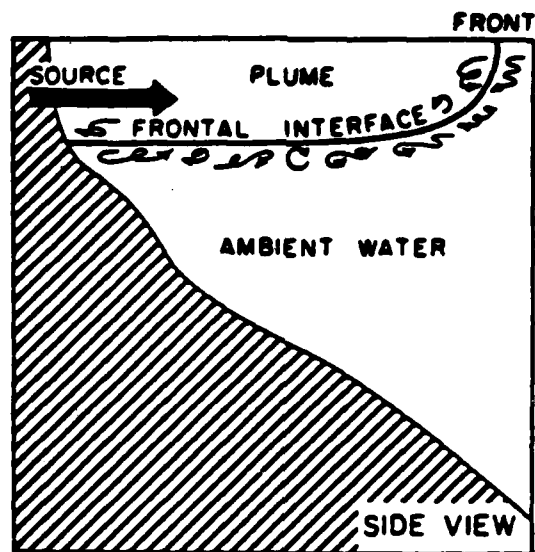


FIGURE 4. Schematic diagrams of a plume front. Arrows represent zones of convergence. Bowman and Iverson (1977)

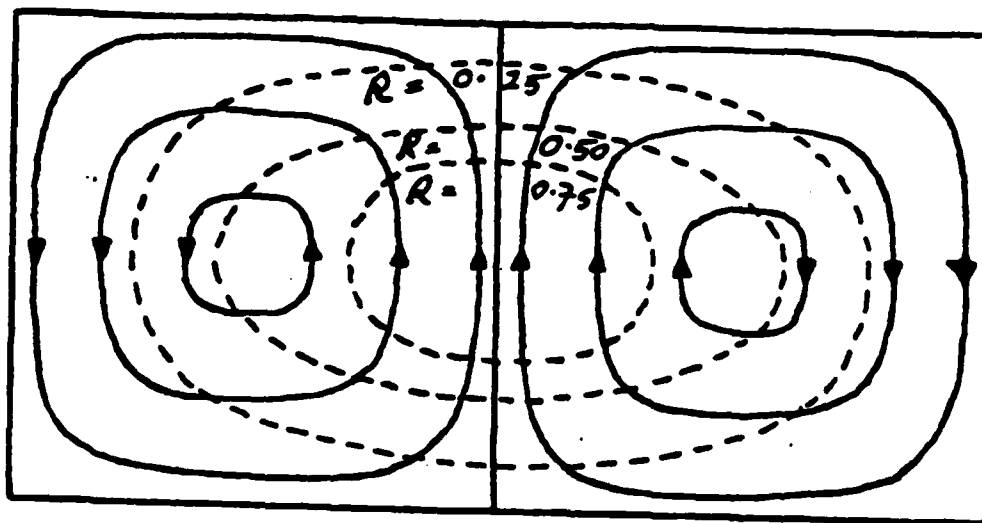


FIGURE 5. Diagram of streamlines in Benard cells showing retention boundaries for three values of R . Stommel (1949)

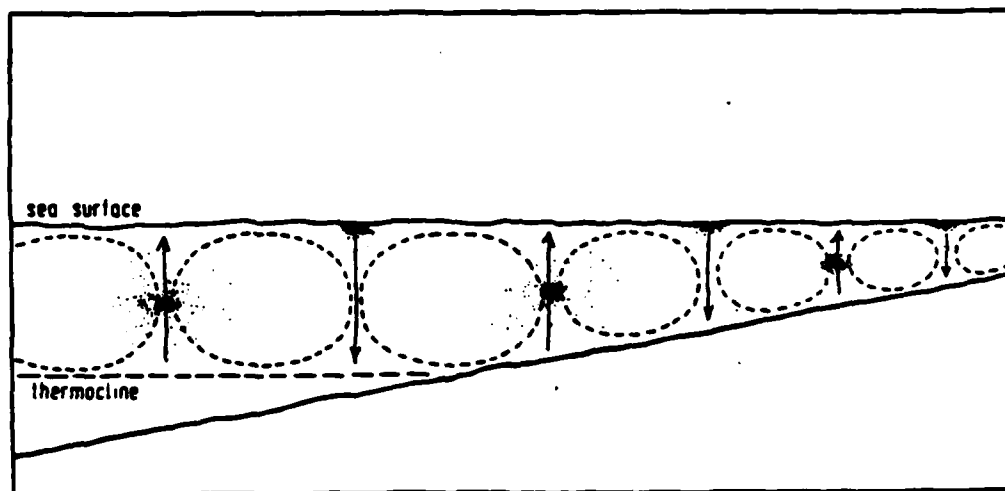


FIGURE 6. Convection cells over a thermocline and shoaling bottom showing regions of accumulation for non-motile organisms with positive sinking velocity (mid-depth, upwelling zones) and motile or buoyant organisms (surface, downwelling zones). Wyatt (1975)

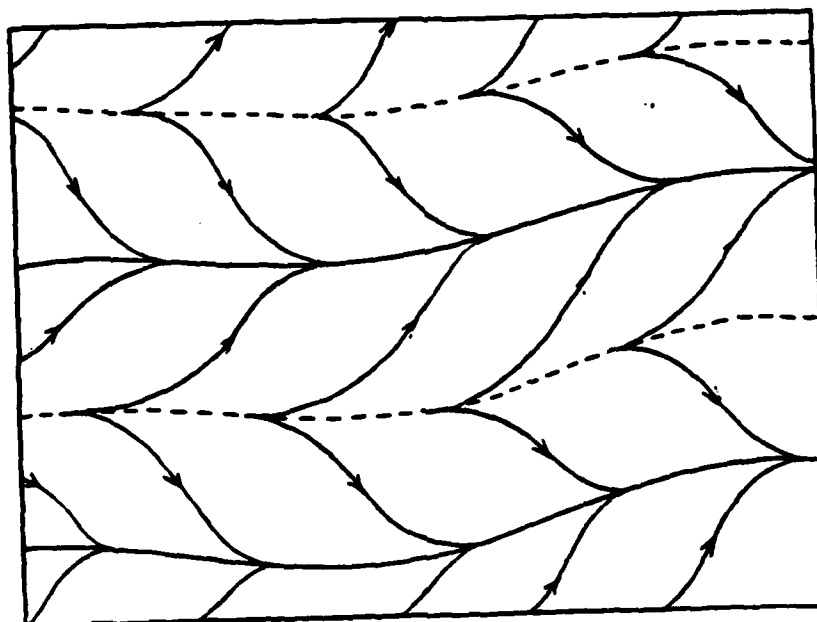


FIGURE 7. Surface view of streamlines of Langmuir cells. Solid lines represent zones of convergence, broken lines represent zones of divergence. Wyatt (1975)

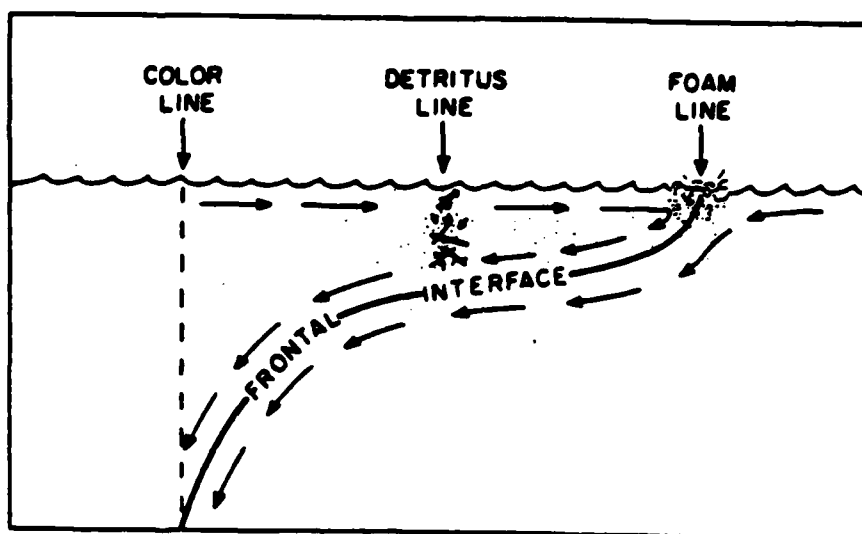


FIGURE 8. Cross-section of a convergent frontal zone showing three visible boundaries, a color front, a detritus line, and a foam line. Bowman and Iverson (1977)

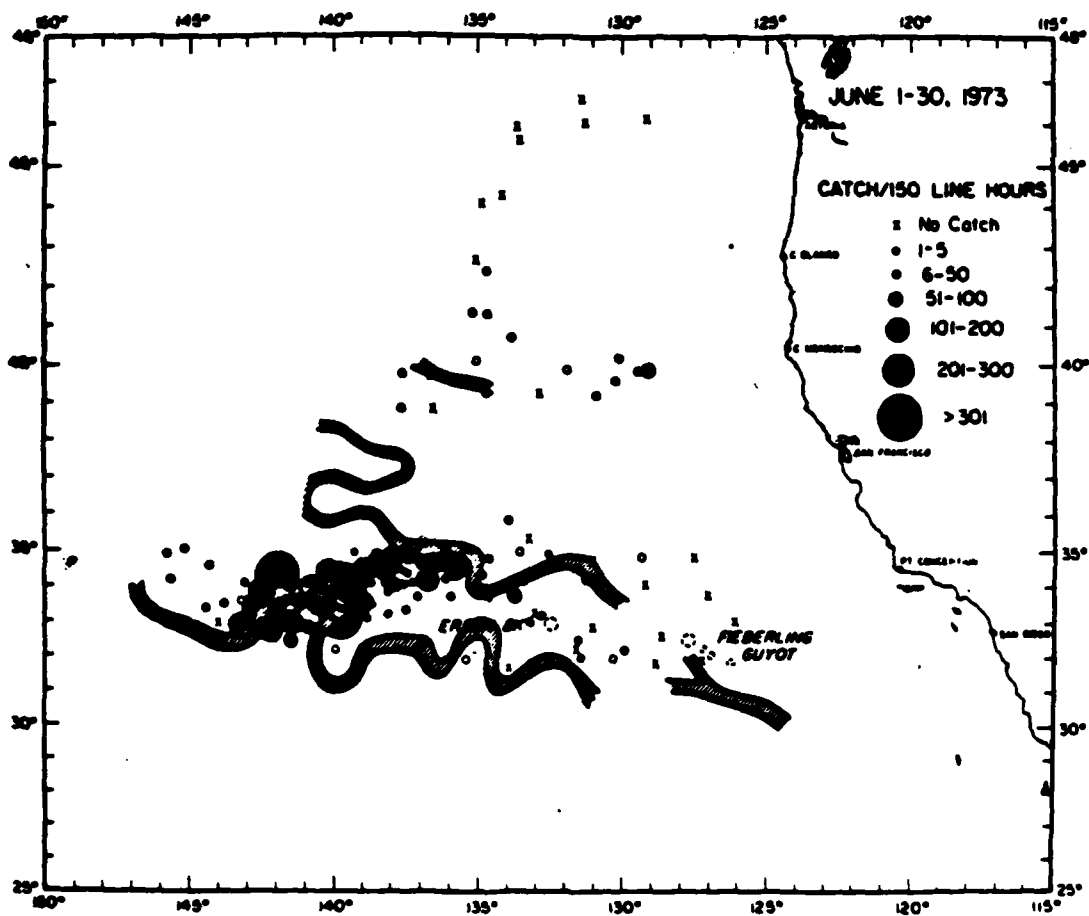


FIGURE 9. Relationship between albacore tuna catch data and fronts (shaded) in eastern Pacific Ocean. Laurs and Lynn (1977)

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